

Comparative histology of caniniform teeth in some predatory ichthyophagous teleosts

by

Megann TEXEREAU (1), Damien GERMAIN* (1) & François J. MEUNIER (2)



© SFI
Received: 8 Dec. 2017
Accepted: 29 Jan. 2018
Editor: O. Otero

Key words

Teleosts
Osteodentine
Orthodentine
Vasodentine
Histology
3D-Tomography

Abstract. – In the present study, the combined use of classical histological and 3D reconstruction methods allows us to characterize the structural organization of different types of dentine in five species of predatory teleosts. The examination evidences the presence of vasodentine and of plicidentine in the perciform *Dissostichus eleginoides* Smitt, 1898 and the presence of osteodentine in three other species of Perciformes without any plicidentine, *Thyrstes atun* (Euphrasen, 1791), *Sphyræna guachancho* Cuvier, 1829, *Lepidopus caudatus* (Euphrasen, 1788), as well as in an esociform species (*Esox lucius* Linnaeus, 1758). Histological methods are shown here to be useful combined with 3D imaging techniques to precise the organization of teleost tooth tissues, and more generally to study morphofunctional adaptation to the diet in both paleontological and neontological contexts.

Résumé. – Histologie comparée de dents caniniformes chez des téléostéens prédateurs ichthyophages.

Dans le présent travail, l'utilisation combinée des méthodes histologiques classiques et des méthodes de reconstruction 3D a permis de caractériser précisément l'organisation structurale des différents types de dentine chez cinq espèces de téléostéens prédateurs. Ainsi, l'examen a montré la présence de vasodentine et de plicidentine chez le Perciforme *Dissostichus eleginoides* Smitt, 1898, d'ostéodentine mais pas de plicidentine chez trois espèces de Perciformes (*Thyrstes atun* (Euphrasen, 1791), *Sphyræna guachancho* Cuvier, 1829 et *Lepidopus caudatus* (Euphrasen, 1788)) ainsi que chez une espèce d'esociforme (*Esox lucius* Linnaeus, 1758). Les méthodes histologiques se sont révélées utiles lors de cette étude et, dans le cadre plus général d'études néontologiques et paléontologiques, elles doivent être utilisées en complément des nouvelles techniques d'imagerie tridimensionnelle pour apporter des précisions sur l'organisation interne des dents des téléostéens et des poissons en général, notamment sur des questions d'adaptations morphofonctionnelles liées au régime alimentaire.

For more than a century and a half, several studies have investigated the histological organization of teleostean teeth (e.g. Owen, 1854; Tomes, 1878; Lison, 1954; Peyer, 1968). However, even if there are about 33,700 teleost species identified so far (Froese and Pauly, 2017), descriptive studies on their dental histology have been limited to only about a hundred. So today, the external morphology of teleost teeth is much better documented when compared to their microstructure. This is notably the case of the histological organization of the dentine and of the attachment between the tooth and its bone support. Throughout literature, many histologists of the 19th and 20th centuries were interested in dentine and its internal organization. Dentine is a mineralized tissue in the teeth of vertebrates that is produced by odontoblasts (Francillon-Vieillot *et al.*, 1990). It is often associated with an external hypermineralized tissue, *i.e.* enamel or enameloid. Odontoblasts recede centripetally to the matrix synthesis front into the pulpar cavity, leaving behind cytoplasmic processes, also called Tomes fibres, contained in a canaliculus and constituting the orthodentine (e.g. Lison, 1954; Peyer, 1968).

In teleosts, there is significant polymorphism of the dentine, giving rise to several categories of tissues (Ørving, 1967). The most common dentine is orthodentine. It is characterized by the presence of a series of odontoblastic tubules organized orthogonally to the pulpar surface (Lison, 1954; Bergot, 1975; Sire *et al.*, 2002, 2009). It has been described in Sarcopterygii such as in the coelacanth (*Latimeria chalumnae* Smith, 1939) (Castanet *et al.*, 1975; Meunier *et al.*, 2015b) and in Teleostei belonging to the orders Anguilliformes (genus *Conger* Bosc, 1817) and Osteoglossiformes (*Arapaima gigas* (Schinz, 1822)) (Lison 1954; Sire *et al.*, 2009; Meunier *et al.*, 2015a). A second type, called vasodentine, was proposed by Tomes (1878) and later studied by Fischer (1938). It has long been considered exclusive to certain teleostean fishes, *i.e.* Gadidae and Ostracionitidae (Tomes, 1899; Lison, 1954). It is characterized by the presence of anastomosing blood vessels in the fundamental substance of the dentine and the lack of odontoblastic canaliculi (Tomes, 1878; Peyer, 1968). A third category of dentine is the osteodentine, which is assimilated to an intermediate between orthodentine and bony tissue, and is

(1) CR2P (MNHN-CNRS-UPMC), Département Origines et Évolution, Muséum national d'Histoire naturelle, CP 038, 57 rue Cuvier, 75231 Paris CEDEX 05, France. [megann.texereau@edu.mnhn.fr]

(2) BOREA (CNRS- MNHN-IRD-UPMC), Département Adaptations du Vivant, Muséum national d'Histoire naturelle, CP 026, 43 rue Cuvier, 75231 Paris CEDEX 05, France. [francois.meunier@mnhn.fr]

* Corresponding author [damien.germain@mnhn.fr]

characterized by both blood vessels and odontoblastic tubules that enter in the dentine walls of the vascular canals (Lison, 1954; Bergot, 1975).

Beside the fundamental types of dentine encountered in teleost fishes, dentine may display a particular spatial organization called plicidentine, first described by Owen (1841 in Tomes, 1878). Placed at the base of the tooth, the plicidentine is characterized by more or less regular folds that project into the pulpar cavity. Independently from the histological type of the dentine, the plicidentine organization appears to be generally associated with canine-like morphology of predators. It has been observed in numerous extant and extinct carnivore sarcopterygians (*e.g.* Lison, 1954; Ørvig, 1967; Peyer, 1968; Schultze, 1969, 1970; Maxwell *et al.*, 2011, 2012; Meunier *et al.*, 2015a), and was long considered as a synapomorphy of Sarcopterygii (Lison, 1954; Peyer, 1968; Schultze, 1970; Maxwell *et al.*, 2011). However, histologists of the 19th and 20th centuries have evoked its presence in some actinopterygians. Owen (1854) and Thomasset (1930) reported the existence of plicidentine in *Lophius* (Lophiiformes) and in *Hydrocyon* (Characiformes) but without going into details. Indeed, detailed description of the plicidentine in actinopterygians was long limited to lepisosteiform fish. Their teeth show the unique case known of complex plicidentine in actinopterygian with their basic secondary folds (Peyer, 1968; Schultze, 1970). Peyer (1968) thus thought that it might be very rare among teleosts. However, histological studies lead during the last decade revealed that it is more frequent than supposed among extant and extinct actinopterygians and especially in teleosts (Meunier *et al.*, 2013, 2015a, 2018a, b; Meunier, 2015; Germain *et al.*, 2016). Virtual sections carried out by microtomography on the teeth of *Dissostichus eleginoides* also appear efficient to reveal the existence of plicidentine composed of primary folds (Germain *et al.*, 2016). A typology of plicidentine was first established by Schultze (1969, 1970). He recognized three subcategories of plicidentine (polyplocodont, eusthenodont, dendrodont) based on the degree and regularity of the dentine folding and other surrounding tissues. The plicidentine in teleosts is less complex when compared to fossil sarcopterygians, and does not belong to any of the subcategories defined by Schultze (1969, 1970). It consists in simple primary folds of the wall of the dentine into the pulpar cavity that are frequently limited to the base of the cavity; it belongs to a fourth subcategory, *i.e.* simplexodont plicidentine, defined by Meunier *et al.* (2015a). The presence of a plicidentine was first interpreted to be a morphofunctional adaptation of predatory fish to enhance and strengthen the tooth attachment to the jaw (Lauder and Liem, 1983; Maxwell *et al.*, 2011; Meunier, 2014). However, the plicidentine was also recently found in the molariform teeth of an African electric fish, the mormyrid *Hyperopisus bebe* (Lacépède, 1803) (Germain *et al.*, 2016; Meunier *et al.*, 2018a).

The aim of this study is to characterize the internal structure of the teeth of several teleost ichthyophagous predators and refine the description of their plicidentine by using conventional histology techniques in association with 3D modelling techniques, notably to discuss further the meaning of the various tooth organization in these fishes. Moreover, this double methodological approach will allow in the background to compare the relative advantages of each method to describe tooth inner structure and address evolutionary questions. We have included the study of the teeth of five emblematic predatory teleosts: those of the pike, *Esox lucius* Linnaeus, 1758 (Esocidae), the osteodentine of which has long been known (Lison, 1954) and thus used as reference to compare with the teeth of four perciforms: the toothfish, *Dissostichus eleginoides* Smitt, 1898 (Nototheniidae), whose teeth show axial ridges on the external surface suggesting the presence of the plicidentine (Germain *et al.*, 2016); the scabbardfish, *Lepidopus caudatus* (Euphrasen, 1788) (Trichiuridae), a snake mackerel, *Thyrssites atun* (Euphrasen, 1791) (Gempylidae), and the barracuda, *Sphyræna guachancho* Cuvier, 1829 (Sphyrænidae).

MATERIAL AND METHODS

Material

The thin sections are deposited in the MNHN collections. The information available on the source specimen are given: MNHN-Histos 2336, 2337: *Esox lucius* Linnaeus, 1758 (Esocidae; Esociformes; Teleostei); 56 cm (SL): premaxilla. MNHN-Histos 2345 to 2346: *Lepidopus caudatus* (Euphrasen, 1788) (Trichiuridae; Perciformes; Teleostei); 134 cm (SL): premaxilla. MNHN-Histos 2338 to 2341: *Thyrssites atun* (Euphrasen, 1791) (Gempylidae; Perciformes; Teleostei); 70-80 cm (SL): premaxilla. MNHN-Histos 2331, 2332: *Sphyræna guachancho* Cuvier, 1829 (Sphyrænidae; Perciformes; Teleostei); 100 cm (TL): premaxilla. MNHN-Histos 2342 to 2344: *Dissostichus eleginoides* Smitt, 1898 (Nototheniidae; Perciformes; Teleostei); female specimen, 136.4 cm (TL); 120 cm (SL), (Austral Ocean): premaxilla.

Methods

The heads were dissected then soaked in boiled water to remove the flesh. The disarticulated premaxillae dried in the open air. Longitudinal and cross sections are obtained at different levels of the tooth and used to characterize the microstructural organization of the teeth.

Ground sections

The bones collected were cleaned and degreased with ethanol. Then, they were immersed in a polyester resin (Araldite 20 / 20B). After 48 h of drying in an incubator, the bones imbedded in the resin were sawed into thin slices.

Depending on availability of tooth samples several serial transverse and longitudinal sections relative to the long axis of the tooth were realized. After polishing, the surfaces of interest of different sections were glued on thin plates of glass. The slides were then polished to obtain a thickness of 50 to 60 μm . The thin slices were observed under an optical microscope in transmitted natural and polarized light.

CT-scan and 3D-reconstruction

The teeth and their supporting bone were X-rayed utilizing a Computed Tomography (CT) imaging system (AST-RX platform and Ge Sensing and Inspection Technologies phoenix-ray vltomelx L240-180 CT scanner) at the MNHN, with nanofocus RX 180kV/15W source and a 400×400 mm detector with a matrix of 2024 pixels (pixel size: 200×200 μm).

For all scans, 3000 images were acquired with the following parameters: voltage 70kV, current 180 μA , exposure 500 ms, with a 0.3 mm copper filter. The micro-CT data were processed utilizing datoslx reconstruction software (Phoenixlx-ray, release 2.0) and then exported as a 16 bit TIFF image stack. VG studio max software (Volume Graphics, release 2.2) was used for the virtual slice visualization and 3D rendering.

The reconstructed voxel sizes were the following: *Esox lucius*, 12.5 μm ; *Lepidopus caudatus*, 20.5 μm ; *Thyrstites atun*, 20.5 μm ; *Sphyræna guachancho*, 15.0 μm and *Dissostichus eleginoides*, 16.0 μm .

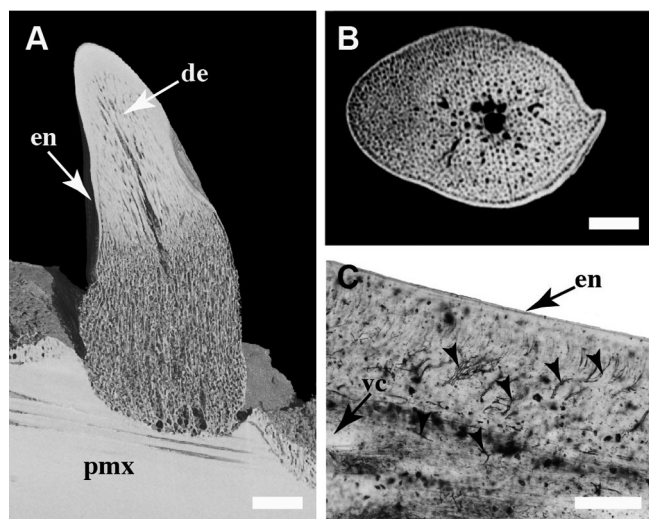


Figure 1. – *Esox lucius* (Esocidae). **A**: 3-D reconstruction of the premaxilla (pmx) with a virtual axial section of a caniniform tooth showing vascularized dentine (de) covered with a thin enameloid (en) layer; **B**: Virtual cross section of the tooth caniniform in A having many elementary units, denteone organized around the vascular canals; **C**: Detail of a longitudinal section (MNHN-Histos 2337 in natural transmitted light) showing many odontoblastic canaliculi (arrowhead) and vascular canals (vc). Scale bars: A = 5 mm; B = 2 mm; C = 50 μm .

RESULTS

3D-reconstruction

CT-scans show that the pulpar cavities of *Esox* (Fig. 1A, B), *Lepidopus* (Fig. 2A, B), *Thyrstites* (Fig. 3A, B) and *Sphyræna* (Fig. 4A) are completely filled with dentinal tissues. On the contrary, virtual sections in the tooth of *Dissostichus* show a weakly developed plicidentine (Fig. 5B) in the pulpar cavity.

Except in *Dissostichus*, all taxa exhibit longitudinal vascular canals in the whole height of the pulpar dentine. In *Dissostichus*, vascular canals display an oblique orientation. Although vascular canals are clearly distinguished on the virtual sections of each sample, the odontoblastic canaliculi remain invisible at these scales, i.e. with voxel size over 10 μm (Figs 1B, 2B, 3B, 5B).

Histology

In the five species investigated, jaw teeth display a dentine cone around the pulpar cavity and they are covered with a thick layer of enameloid (Figs 1A, 2A, 3A, 4A, 5C). The pulpar cavity is relatively reduced in height and its diameter decreases progressively from the base to the apex of the tooth. Teeth are fixed on their supporting bone by a bone of attachment.

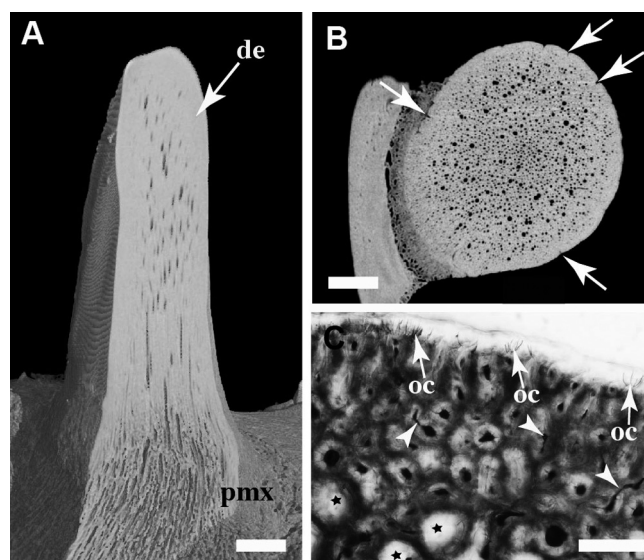


Figure 2. – *Lepidopus caudatus* (Trichiuridae). **A**: 3-D reconstruction of the premaxilla (pmx) with a virtual axial section of a caniniform tooth showing vascularized dentine (de) covered with a thin enameloid layer; **B**: Virtual cross section of the tooth caniniform in A having many denteones; **C**: Detail of a cross section (MNHN-Histos 2347 in natural transmitted light) showing the presence of denteones (asterisks) and anastomosed vascular canals (arrowheads). Odontoblastic canaliculi (oc) take an orientation perpendicular to the axis of the tooth as it approaches the outer surface of the tooth. Scale bars: A = 5 mm; B = 2 mm; C = 50 μm .

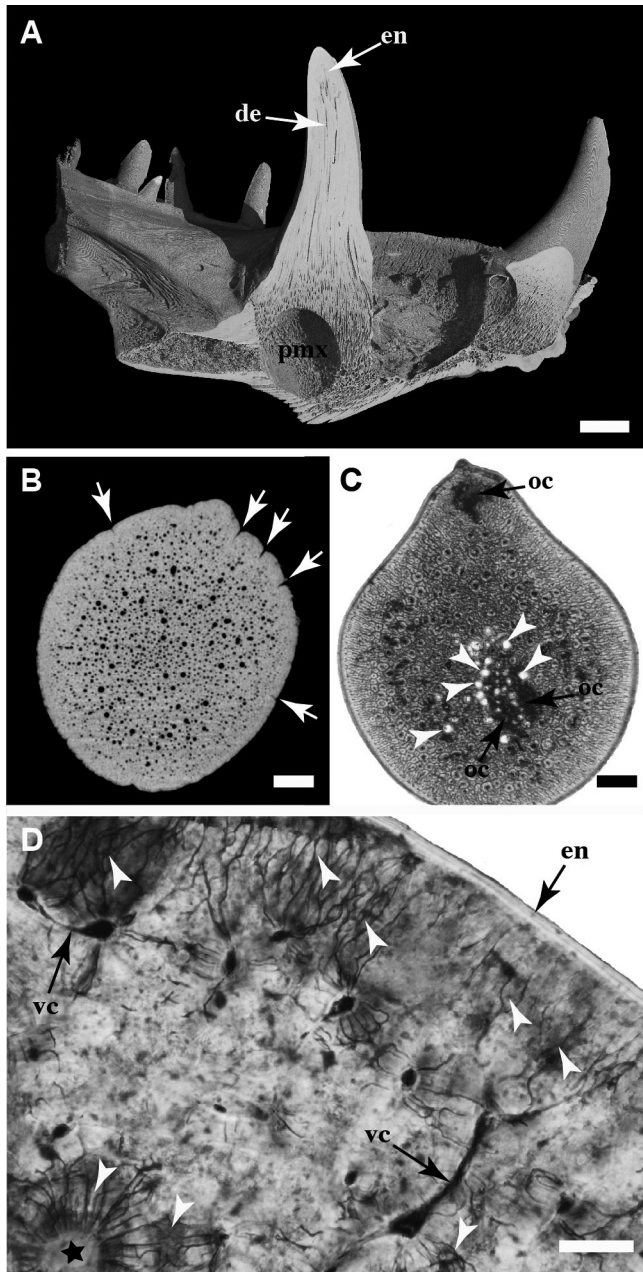


Figure 3. – *Thyrsites atun* (Gempylidae). **A**: 3-D reconstruction of the premaxilla (pmx) with a virtual axial section of a caniniform tooth showing vascularized dentine (de) covered with a thin enameloid layer and a cap of enameloid (en); **B**: Virtual cross section of a caniniform tooth showing dentine folds (white arrows) and many denteones at the dentine; **C**: Cross section (MNHN-Histos 2340 in natural transmitted light) showing the presence of many denteones (arrowheads) and many branches of odontoblastic canaliculi (oc), some of these branches form highly visible plumes (arrows); **D**: Detail of the cross section in B (MNHN-Histos 2340 in natural transmitted light) showing the presence of denteones (asterisks), many ramified odontoblastic canaliculi (oc) (white arrowheads) and anastomosed vascular canals (vc). Scale bars: A = 5 mm; B, C = 2 mm; D = 20 μ m.

Esox lucius, *Lepidopus caudatus*, *Thyrsites atun* and *Sphyræna guachancho*

The various sections obtained from *Esox lucius* (Fig. 1), *Lepidopus caudatus* (Fig. 2), *Thyrsites atun* (Fig. 3) and in *Sphyræna guachancho* (Fig. 4) mainly show common features. In these fishes, the dentine includes odontoblastic processes housed in canaliculi. These canaliculi tend to decrease in number from the base to the apical region of the tooth. In addition, they arborize in several branchings and sometimes emit a panache of highly fine processes that establish connections with each other (Figs 1C, 2C, 3D, 4B, C). The odontoblastic canaliculi follow a general direction parallel to the axis of the tooth except when they approach the external surface of the tooth where they arrange perpendicularly direction (Figs 2C, 3D, 4C). In addition to the odontoblastic canaliculi, a vascular system is also observed in the thickness of the teeth with numerous vascular canals, most of them being anastomosed (Figs 1C, 2C, 3D, 4B, C). Such an organization, with odontoblastic canaliculi and vascular canals present, characterizes a specific variety of dentine named osteodentine (Lison, 1954). It is composed of simple units, the denteones (Francillon-Vieillot *et al.*, 1990), organized around a vascular canal (Figs 1B, 2B, C, 3B, C). They are separated from each other by bands of calcified fibrous tissue composed of collagen fibres.

Examination in polarized light might evidence nicely the spatial organization of these fibres. In *Sphyræna guachancho*, the observation of a cross section in polarized light revealed their presence in dentine matrix. In fact, these fibres surrounding the vascular canals, are highly birefringent and appear in bright tint. However, in longitudinal section, they do not polarize and appear in dark. These collagen fibres are aligned parallel to each other and are therefore following a trajectory parallel to the direction of vascular canals and to the long axis of the tooth (Fig. 4B, C).

The teeth of these four predators do not show dentin folds projecting into the base of the tooth, *i.e.* plicidentine is absent. The different sections show an enameloid layer around the teeth. This layer thickens gradually toward the apex of the tooth to the point that for some specimens, it forms a real cap of enameloid, the so-called cap acrodine (Figs 1A, 2B, 3A, 4A). A thick layer of enameloid is noticed on the cutting edge of the teeth in *Thyrsites atun* (Fig. 3B, C).

Dissostichus eleginoides

In this fish, no odontoblastic process is observed on any longitudinal or transverse histological section (Fig. 5D, E). However, dentine shows thin perforations (Fig. 5B) and/or canals (Fig. 5C). Several anastomosing vascular canals leave the pulpar cavity following a direction parallel to the main axis of the tooth (Fig. 5D). The mere presence of a vascular system in the tooth thickness and the absence of odontoblastic canaliculi are characteristic of a specific variety of

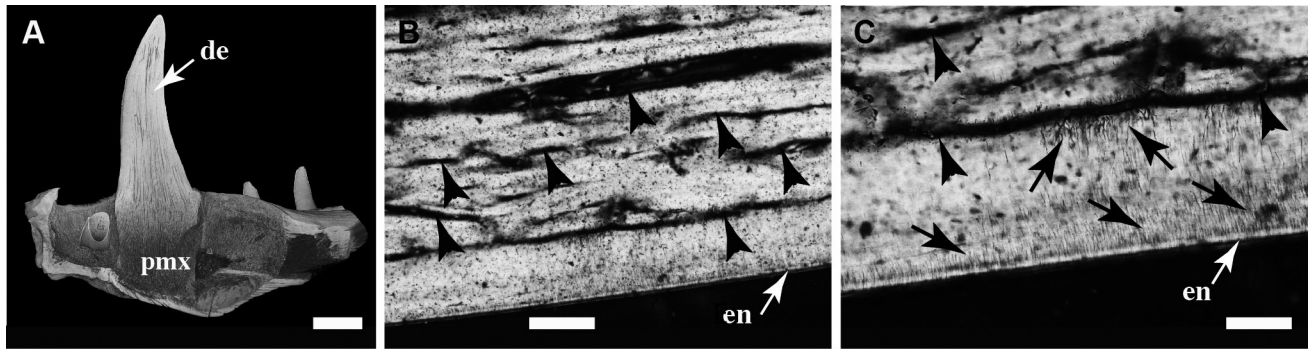


Figure 4. – *Sphyraena guachancho* (Sphyaenidae). **A**: 3-D reconstruction of the premaxilla (pmx) with a virtual axial section of a caniniform tooth showing vascularized dentine (de) covered with a thin enameloid layer and a cap of enameloid (en); **B**: Longitudinal section (MNHN-Histos 2332 in polarized light) showing the spatial organization of collagen fibers that follow a trajectory parallel to the direction of the vascular canals and to the main axis of the tooth (black arrowheads); the tooth is covered with a thin enameloid (en) layer; **C**: Detail of the longitudinal section in B (MNHN-Histos 2332 in polarized light) showing the presence of odontoblastic canaliculi perpendicular to the tooth area (black arrowheads); the tooth is covered with a thin enameloid layer (en). Scale bars: A = 5 mm; B = 10 µm; C = 40 µm.

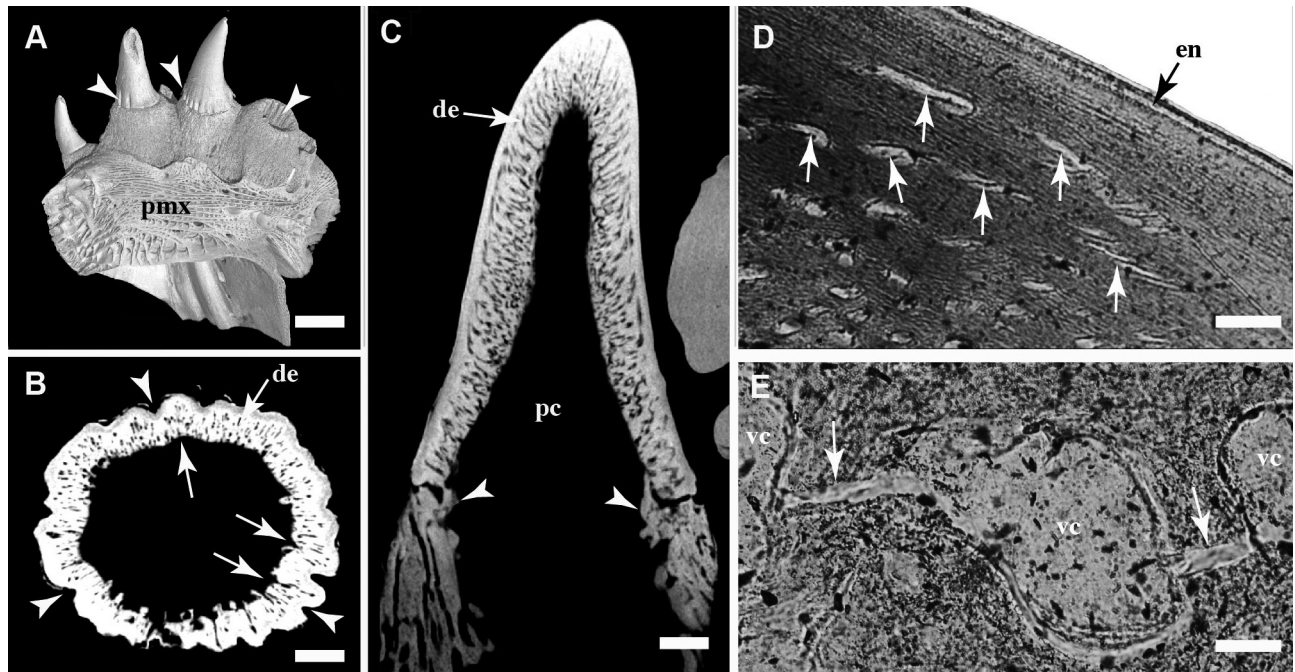


Figure 5. – *Dissostichus eleginoides* (Nototheniidae). **A**: Virtual model of the whole left premaxilla (pmx) showing the external aspect of the three caniniform teeth with external basal ridges (arrowheads); a fourth broken tooth shows folds in the pulpar cavity (white arrows); **B**: Virtual cross-section showing dentine folds (white arrows) and external ridges (white arrowheads); the dentine (de) core of the tooth is perforated; **C**: Virtual axial section of the largest tooth showing thin cavity and canals in the dentine (de); the tooth is covered with a thin enameloid (en) layer and forms a cap at the apex of the tooth; white arrowheads point to fold in the pulpar cavity (pc); **D**, **E**: Detail of a longitudinal (D) and transverse (E) sections (MNHN-Histos 2344 (D), MNHN-Histos 2342 (E) in natural transmitted light) showing the presence of many vascular canals anastomosed (white arrows); no odontoblastic tubules is present; the tooth is covered with a thin enameloid layer (en). Scale bars: A = 5 mm; B = 2 mm; C = 1 mm; D = 10 µm; E = 40 µm.

dentine, the vasodentine (Lison, 1954; Herold, 1970). On the virtual sections, a plicidentine composed of simple folds is present in the basal third of the pulpar cavity (Fig. 5A-C). Meanwhile, enameloid is present in a thin collar at the periphery of the tooth and thickens toward the top forming the cap acrodine (Fig. 5C).

DISCUSSION AND CONCLUSION

Dentine characterization and methodological issues

Recent studies using 3D-reconstruction have proved their validity to reveal the true spatial organization of dentine in the living coelacanth (Meunier *et al.*, 2015b), in the living basal Actinopterygii (Meunier and Brito, 2017; Germain

and Meunier, 2018), and in various teleostean fishes (Germain *et al.*, 2016). Yet the virtual 2D-reconstruction is far not as accurate as the classical techniques (ground sections of undemineralized material) to decipher the microscopic histology of dentine tissue. In the present study, the use of conventional techniques combined with 3D-reconstruction methods allows to characterize precisely the spatial organization of teeth, including the presence or absence of the plicidentine: no plicidentine was detected on the 3D-reconstruction of the teeth of *Esox lucius*, *Lepidopus caudatus*, *Sphyaena guachancho* and *Thyrstites atun*.

Correlation between the presence of plicidentine and the tooth morphology

The lack of plicidentine in *Esox lucius*, *Lepidopus caudatus*, *Sphyaena guachancho* and *Thyrstites atun* is consistent with the outer smooth appearance of the basis of their teeth. Reversely, virtual reconstructions of the teeth of *Dissostichus eleginoides* with ridges on their outer surface show the existence of folds in the pulpar cavity of their teeth: plicidentine is present like suggested by their outer appearance (Fig. 5B). This latter result agrees with the hypothesis of Meunier *et al.* (2015b), that the presence of external ridges at the base of a tooth may reveal the inner organization and thus the presence of plicidentine. Similar results were yet obtained by Meunier *et al.* (2015a: fig. 2) in the characiform fish *Hoplias aimara* (Valenciennes, 1847) (Characiformes) and in the anglerfish *Lophius piscatorius* (Meunier, 2015). Conversely, the absence of outer ridges is not sufficient to deduce the absence of plicidentine. Effectively the smooth teeth from the lingual plate of *Arapaima gigas* have plicidentine (Meunier *et al.*, 2013), as well as the smooth caniniform teeth of *Latimeria chalumnae* (Meunier *et al.*, 2015b). To conclude on that point, the inner spatial organization seems to be deduced from the outer aspect, but only in the case of a plicated morphology at the base, but in the case of a smooth outer surface, a section is necessary to conclude on the pulpar surface organization.

Correlation between dentine features and ichthyophagy

The five studied species belong to various living fish-eating predators distributed in the phylogenetic tree of teleost fishes (Betancur-R *et al.*, 2013, 2017). These teleosts have “caniniform” teeth adapted to their diet. These teeth consist of several superimposed layers. The most superficial, hypermineralized, constitute the enameloid that overlaps a dentine layer a hard tissue (Francillon-Vieillot *et al.*, 1990).

The sample of this study was not designed to confirm or invalidate the hypothesis that the appearance of plicidentine is related with ichthyophagy in teleosts (Meunier *et al.*, 2015a). If further confirmed, the presence of plicidentine in actinopterygian predators is probably linked to a morpho-functional adaptation possibly involving phenotypic plastic-

ity. Plicidentine significantly increases the attachment surface of the tooth to the basal bone, which probably strengthens the teeth to resist dental constraints when catching prey (Lauder and Liem, 1983; Meunier *et al.*, 2013; Germain *et al.*, 2016). However, we show here that plicidentine is not compulsory in ichthyophagous teleosts, and we suggest that a strengthening of the teeth can also be achieved by an infilling of the pulpar cavity with vasodentine or osteodentine.

While Tomes proposed in 1878 the current definition of vasodentine, it was only half a century later that its histogenesis was studied by Fisher (1936 in Lison, 1954). This dental tissue was considered to be exclusive to some teleosts (Gadidae and Ostracionitidae) (Lison, 1954). It is characterized, (i) by the presence of anastomosed vascular canals in the dentine matrix (Tomes, 1878; Peyer, 1968), (ii) the disappearance of odontoblastic canaliculi. However, the histological sections of *Dissostichus eleginoides* teeth and the 3D reconstructions show the absence of odontoblast processes and thus confirms the presence of vasodentine in this species (Germain *et al.*, 2016). Concerning osteodentine, Peyer (1968) assumption was rapidly challenged with the observation of osteodentine in *Esox Lucius* (Esociformes) by several authors (Lison, 1954; Herold and Landino, 1970; Herold, 1971), which is confirmed by our work. Globally, we assume that the variety of dentine in different predatory teleosts does not correlate with their diet and has certainly a low or no direct adaptive value on that aspect.

Finally, the use of classical techniques of histology (observation of ground sections of undemineralized material) has allowed the characterization of the different types of dentin in fish-eating teleosts. However, these techniques have limitations since they contribute to the deterioration of specimens and moreover they limit our understanding of the spatial organization of the tissue, unlike three-dimensional imaging techniques. Among the whole described teleosts (Froese and Pauly, 2017), only three categories of dentine have been described (Germain *et al.*, 2016). The combined systematic use of these two complementary methods would probably allow to better document dental histology of modern and fossil fish when material is available (Meunier *et al.*, 2013).

Acknowledgments. – This study was supported by the “Muséum national d’Histoire naturelle” (MNHN, Paris) with a grant “ATM Formes, 2014” and the “AST-RX plateau d’Accès Scientifique à la Tomographie à Rayons X du MNHN” for CT-Scanning, performed by Miguel Garcia-Sanz and Maïté Adam, and the “atelier Tomographie du CR2P” (Florent Goussard). We would also like to thank Séverin Morel (UMR 7207, CR2P, IMSI-UMS 2700 MNHN-CNRS, Muséum national d’Histoire naturelle) for his technical assistance in the preparation of ground sections. We acknowledge Dr Guy Duhamel (UMR 7208, BOREA, Dep. Adaptations du Vivant, MNHN, Paris) for *Dissostichus* and Dr Khady Diouf-Goudiaby (Univ. Dakar, Senegal) for *Sphyaena guachancho*. Many thanks to the anonymous referees for their valuable comments.

REFERENCES

- BERGOT C., 1975. - Mise en évidence d'un type particulier de dentine chez la truite (*Salmo* sp., Salmonidés, Téléostéens). *Bull. Soc. Zool. Fr.*, 100(4): 587-59.
- BETANCUR-R.R., BROUGHTON R.E., WILEY E.O. *et al.* [24 authors], 2013. - The tree of life and a new classification of bony fishes. *PLOS Currents Tree of Life*, 2013 Apr. 18, Edition 1. doi: 10.1371/currents.tol.53ba26640df0ccae75bb165c8c26288.
- BETANCUR-R.R., WILEY E.O., ARRATIA G., ACERO A., BAILLY N., MIYA M., LECOINTRE G. & ORT' G., 2017. - Phylogenetic classification of bony fishes. *BMC Evol. Biol.*, 17(162). doi: 10.1186/s12862-017-0958-3.
- CASTANET J., MEUNIER F., BERGOT C. & FRANCOIS Y., 1975. - Données préliminaires sur les structures histologiques du squelette de *Latimeria chalumnae*. I – Dents, écailles, rayons de nageoires. In: Coll. Int. CNRS, Problèmes actuels de Paléontologie. Évolution des Vertébrés, Paris, 4-9 juin 1973, pp. 159-168.
- FRANCILLON-VIEILLOT H., BUFFRÉNIL V. (de), CASTANET J., GERAUDIE J., MEUNIER F.J., SIRE J.Y., ZYLBERGERG L. & RICQLES A. (de), 1990. - Microstructure and mineralization of vertebrate skeletal tissues. In: *Skeletal Biomineralization; Patterns, Processes and Evolutionary Trends* (Carter J.G., ed.), pp. 471-548. New York: Van Nostrand Reinhold.
- FISCHER H., 1938. - Über Bau und Entwicklung des Gadidaezahnes. *Z. Zellforsch.*, 27: 726-744.
- FROESE R. & PAULY D., 2017. - Fishbase: www.fishbase.org. Accessed October 2017.
- GERMAIN D. & MEUNIER F.J., 2018. - Teeth of Polypteridae and Amiidae have plicidentine organisation. *Acta Zool.*, in press. doi.org/10.1111/azo.12237).
- GERMAIN D., MONDÉJAR-FERNANDEZ J. & MEUNIER F.J., 2016. - The detection of weakly developed plicidentine in teleost teeth using 3D tomography. *Cybium*, 40(1): 75-82.
- HEROLD R.C., 1970. - Vasodentine and mantle dentine in teleost fish teeth. A comparative microradiographic analysis. *Arch. Oral Biol.*, 15: 71-85.
- HEROLD R.C., 1971. - Osteodentinogenesis. An ultrastructural study of tooth formation in the pike (*Esox lucius*). *Z. Zell.*, 112: 1-14.
- HEROLD R.C. B. & LANDINO L., 1970. - The development and mature structure of dentine in the pike, (*Esox lucius*), analyzed by bright field, phase and polarization microscopy. *Arch. Oral Biol.*, 15: 747-760.
- LAUDER G.V. & LIEM K.F., 1983. - The evolution and interrelationship of the Actinopterygian fishes. *Bull. Mus. Comp. Zool.*, 150(3): 95-197.
- LISON L., 1954. - Les dents. In: *Traité de Zoologie* (Grassé P.P., ed.), pp. 791-853. Paris: Masson.
- MAXWELL E.E., CALDWELL M.W. & LAMOUREUX D.O., 2011. - The structure and phylogenetic distribution of amniote plicidentine. *J. Vert. Paleontol.*, 31(3): 553-561.
- MAXWELL E.E., CALDWELL M.W. & LAMOUREUX D.O., 2012. - Tooth histology attachment, and replacement on the ichthyopterygia reviewed in an evolutionary context. *Paläontol. Z.*, 86(1): 1-14.
- MEUNIER F.J., 2014. - La plicidentine, une adaptation à la prédation chez les Ostéichthyens ? Actes des XV^e Journées Tunisiennes des Sciences de la Mer & 3^e rencontre Tuniso-française d'Ichtyologie (Mahdia, Tunisie, 2013). *Bull. Inst. Natl. Sci. Tech. Mer*, Salammbô, 17: 37-42.
- MEUNIER F.J., 2015. - New data on the attachment of teeth in the Angler fish *Lophius piscatorius* (Actinopterygii; Teleostei; Lophiidae). *Cah. Biol. Mar.*, 56(2): 97-104.
- MEUNIER F.J. & BRITO P.M., 2017. - Histological characteristics of lower jaws and oral teeth in the short nose gar, *Lepisosteus platostomus* Rafinesque, 1820 (Lepisosteidae). *Cybium*, 41(3): 279-286.
- MEUNIER F.J., BRITO P.M. & LEAL M.E.C., 2013. - Morphological and histological data on the structure of the lingual toothplate in *Arapaima gigas* (Osteoglossidae; Teleostei). *Cybium*, 37(4): 263-271.
- MEUNIER F.J., DE MAYRINCK D. & BRITO P.M., 2015a. - Presence of plicidentine in the labial teeth of *Hoplias aimara* (Erythrinidae; Ostariophysi; Teleostei). *Acta Zool.*, 96: 174-180.
- MEUNIER F.J., MONDÉJAR-FERNANDEZ J., GOUSSARD F., CLÉMENT G. & HERBIN M., 2015b. - Presence of plicidentine in the oral teeth of *Latimeria chalumnae* (Sarcopterygii; Actinistia; Coelacanthidae). *J. Struct. Biol.*, 190(1): 31-37.
- MEUNIER F.J., GERMAIN D. & OTERO O., 2018a. - A histological study of the lingual molariform teeth in *Hyperopisus bebe* (Mormyridae; Osteoglossomorpha; Teleostei). *Cybium*, 42(1): 87-90.
- MEUNIER F.J. & OTERO O., LAURIN M. 2018b. - Histological study of the jaw teeth in the Devonian actinopterygian †*Cheirolepis canadensis* (Whiteaves). *Cybium*, 42(1): 67-74.
- ØRVIG T., 1967. - Phylogeny of tooth tissues: evolution of some calcified tissues in early Vertebrates. In: *Structural and Chemical Organization of Teeth*, Vol. I (Miles A.E.W., ed.), pp. 45-110. London: Academic Press.
- OWEN R., 1854. - On the principal forms and structures of the teeth. In: *The Principal Forms of the Skeleton and of the Teeth* (Blanchard & Lea, eds), pp. 229-263. Philadelphia: T.K. & P.G. Collins.
- PEYER B., 1968. - Osteichthyes. In: *Comparative Odontology* (Zangerl R., ed.), pp. 80-110. Univ. Chicago Press.
- SCHULTZE H.P., 1969. - Die Faltenzähne der Rhipidistiden Crossopterygier, der Tetrapoden und der Actinopterygier-Gattung *Lepisosteus* nebst einer Beschreibung der Zahnstruktur von *Onychodus* (Strunniiformer Crossopterygier). *Palaeont. Ital. New Ser.*, 35(65): 63-137.
- SCHULTZE H.P., 1970. - Folded teeth and the monophyletic origin of Tetrapodes. *Am. Mus. Nov.*, 2408: 1-10.
- SIRE J.Y., DAVIT-BÉAL T., DELGADO S., VAN DER HEYDEN C. & HUYSEUNE A., 2002. - First-generation teeth in non-mammalian lineages: evidence for a conserved ancestral character? *Microsc. Res. Tech.*, 59: 408-434.
- SIRE J.Y., DONOGHUE P.C.J. & VICKARYOUS M.K., 2009. - Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. *J. Anat.*, 214 : 409-440.
- THOMASSET J.J., 1930. - Recherches sur les tissus dentaires des poisons fossiles. *Arch. Anat. Microsc.*, 11: 6-153.
- TOMES C.S., 1878. - On the structure and development of vascular dentine. *Phil. Trans. R. Soc., Lond.*, 169: 25-47.
- TOMES C.S., 1899. - On differences in the histological structure of teeth occurring within a single family in the Gadidae. *Quart. J. Microsc. Sci.*, 41(4): 459-469.

